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Future marine ecosystem drivers, biodiversity, and fisheries maximum catch potential in Pacific Island countries and territories under climate change

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ABSTRACT

The increase in anthropogenic CO_2 emissions over the last century has modified oceanic conditions, affecting marine ecosystems and the goods and services that they provide to society. Pacific Island countries and territories are highly vulnerable to these changes because of their strong dependence on ocean resources, high level of exposure to climate effects, and low adaptive capacity. Projections of mid-to-late 21st century changes in sea surface temperature (SST), dissolved oxygen, pH, and net primary productivity (NPP) were synthesized across the tropical Western Pacific under strong climate mitigation and business-as-usual scenarios. These projections were used to model impacts on marine biodiversity and potential fisheries catches. Results were consistent across three climate models, indicating that SST will rise by $\geq 3\,^{\circ}C$, surface dissolved oxygen will decline by ≥ 0.01 ml L^{-1}, pH will drop by ≥ 0.3, and NPP will decrease by 0.5 g m^{-2} d^{-1} across much of the region by 2100 under the business-as-usual scenario. These changes were associated with rates of local species extinction of $>$ 50% in many regions as fishes and invertebrates decreased in abundance or migrated to regions with conditions more suitable to their bio-climate envelope. Maximum potential catch (MCP) was projected to decrease by $>$ 50% across many areas, with the largest impacts in the western Pacific warm pool. Climate change scenarios that included strong mitigation resulted in substantial reductions of MCP losses, with the area where MCP losses exceeded 50% reduced from 74.4% of the region under business-as-usual to 36.0% of the region under the strong mitigation scenario.

1. Introduction

Global climate change driven largely by greenhouse gas emissions from anthropogenic activities has modified the physical and chemical properties of the oceans [69]. Growing evidence has shown significant anomalies in temporal fluctuations and spatial distributions of key environmental parameters in both open-oceans and coastal areas [43,50]. Since the 1950s, the global ocean has experienced increases in sea surface temperature (SST), decreases in pH, an expansion of oxygen minimum zones, and a rise in sea level. These oceanographic changes are projected to continue and amplify in the 21st century with an unprecedented rate of change and reaching CO_2 concentrations that have not been experienced since geologic times [35].

These changes in ocean conditions are affecting living marine resources at a global scale. Most fishes and invertebrates are particularly sensitive to changes in ocean conditions because their body temperature and biological performance varies with the environment [60]. Warming temperatures affect ectothermic fishes by accelerating a range of metabolic processes that influence life stage duration, growth rates, energetic demand, and other vital rates [61]. In addition to changing temperatures, ocean acidification, decreasing oxygen concentration, and declining primary productivity also have the capacity to negatively impact fishes and fisheries. Primary productivity is important for sustainable fisheries because phytoplankton is the base of the ocean food web and ultimately provides energy for most organisms in higher trophic levels. Primary productivity is projected to decline in low latitude regions of the ocean due to the fact that warming surface temperatures will increase stratification preventing nutrients at depth from making their way to the surface where they are needed for photosynthesis [13]. Decreases in oxygen concentration can limit the depths that can be occupied by fishes leading to habitat compression. Such changes in the depth distribution of fishes can affect interactions between predators and prey, as well as interactions between fisheries and their target species [62,56]. Ocean acidification negatively affects fishes and fisheries through three mechanisms. First, ocean acidification can alter the sensory perception and behavior of fishes in ways that

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make them increasingly vulnerable to predation [27,54,55]. Second, due to ocean acidification's impact on coral reef calcification, these changes in pH will decrease the amount of habitat available to reef-associated fishes [39,70]. Third, ocean acidification is projected to alter marine food webs through its effects on the calcification, growth, mortality rates, and reproductive success of a variety of marine organisms that serve as prey, predators, and competitors of fishes [45]. In the tropical Pacific, direct effects of ocean acidification and food web impacts are expected to have larger effects on coastal fishes than open-ocean species, such as tuna [15,48].

Overall, marine fishes and invertebrates respond to these changes through shifts in distribution towards higher latitude, deeper water, or generally, toward areas with closer to optimal environmental conditions for the population to survive [44,58,59], and the alteration of their seasonal cycles, such as spawning and migration timing [2,36,37]. Consequently, these biological responses affect biodiversity and important ecosystem services (*e.g.*, fisheries), with changing species composition (*i.e.*, species gains and local extinction resulting from distribution shifts) and regional decreases in fisheries catch potential anticipated as the climate warms [23].

Tropical Pacific areas have been identified as one of the most vulnerable regions in the world's oceans to climate change impacts [8,23]. Biologically adapted to a seasonally more stable environment relative to other parts of the ocean, tropical marine species generally have a narrower tolerance range for temperature [20,60]. This renders tropical species more sensitive to warming and other oceanographic changes [18]. In addition, coral reefs, a critical habitat for many tropical species and fisheries resources, are highly sensitive to small changes in temperature resulting in coral bleaching during heat waves, physical damage from storms, and reduced calcification from ocean acidification [26,39,40].

Socially and economically, most countries in the tropical Pacific are strongly dependent on fisheries for food and livelihoods [4,6,19,33]. Across most countries in this region, fishes contribute > 20% of the animal protein that sustains the human population [32], with this contribution well exceeding 50% on some islands [19]. From an economic perspective, this region's tuna fisheries are especially lucrative, with tuna fishing licenses sold to other countries contributing up to 60% of tax revenues for some Pacific Island countries and territories (PICTs) [9]. Climate fluctuations in this region can also have economic impacts through their effect on the tourism industry, which is strongly related to iconic marine species. Overall, travel and tourism contributed 12% of the GDP and 13% of the employment in Oceania in 2016, making tourism a key sector of the regional economy [74]. The socio-economic vulnerability of the region to marine climate change impacts is also underscored by the fact that the capacity of Small Island Developing States (SIDS) in the tropical Pacific to adapt to or mitigate climate change impacts may be lower than that of developed countries [10,46].

This paper aims to provide an overview of long-term projections of changes in ocean conditions, biodiversity and fisheries that are important to the sustainability of coastal communities in PICTs during the 21st century under climate change. This information is used to highlight the potential level of exposure and sensitivity of these countries to climate change. The paper then discusses the potential impacts of climate change on important biological and social-ecological systems for PICTs.

2. Materials and methods

2.1. Physical and biogeochemical oceanic variables

SST, surface pH, surface oxygen concentration, and vertically integrated (0–100 m) net primary production (NPP) were selected as indicators of changes in ocean physics and biogeochemistry. These variables were selected because changes in these variables are likely to have large impacts on marine species through either direct effects on physiology or alterations of the trophodynamics of marine ecosystems.

Information on these variables was derived from the National Oceanic and Atmospheric Administration (NOAA) Geophysical Fluid Dynamics Laboratory's Earth System Model (GFDL ESM2G; [28,29], the Institute Pierre Simon Laplace model (IPSL-CM5A-MR; [3], and the Max-Planck Institutes Earth System Model (MPI-ESM-MR; [42]. These three climate models were selected since they were developed independently, include all ocean biogeochemical variables of interest, and represent the full spectrum of equilibrium climate sensitivities among models included in the latest Intergovernmental Panel on Climate Change (IPCC) assessment report [1]. GFDL ESM2G has a nominal 1° latitudinal/longitudinal ocean resolution and 63 depth layers. This earth system model uses the TOPAZ2.0 biogeochemical submodel to examine dynamical changes in pH, O_2, and NPP. The IPSL model has a latitudinal/longitudinal ocean resolution that varies between 0.5–2.0° and contains 31 depth layers. It uses the PISCES submodel to track the dynamics of the biogeochemical variables reported upon herein. The MPI model has a latitudinal/longitudinal ocean resolution of 0.4° with 40 depth layers. Ocean biogeochemistry is tracked in MPI using the HAMOCC5.2 submodel. To account for variability between different climate models, our analysis averaged data from these three models together to create a composite projection of future changes.

Data from these models were extracted for three time periods: a baseline period (1980–2000), a mid-century period (2040–2060), and an end-of-century period (2080–2100). Data for twenty-year periods were extracted to minimize the likelihood that a climate change signal would be masked by naturally occurring interannual or decadal climate variability (*e.g.*, El Niño-Southern Oscillation, Pacific Decadal Oscillation). Two climate change emissions scenarios were considered: Representative Concentration Pathways (RCP) 2.6 and 8.5. RCP 8.5 is a high emissions scenario where anthropogenic greenhouse gas and aerosol emissions induce an 8.5 W m^{-2} change in radiative forcing by the year 2100. Under the RCP 2.6 scenario, considerable climate mitigation efforts result in a lower 2.6 W m^{-2} change in radiative forcing by 2100.

2.2. Ocean biodiversity

The projected effects of climate change on species richness were mapped in tropical Pacific regions using an approach similar to Jones and Cheung [44]. Current and future distributions of marine fishes and invertebrates were projected using species distribution models. To identify the environmental niche of 1091 selected species occurring in the tropical Pacific, records of species occurrence were collated from the following publicly accessible databases: the Ocean Biogeographic Information System (OBIS – www.iobis.org), the Intergovernmental Oceanographic Commission (IOC – ioc-unesco.org), the Global Biodiversity Information Facility (GBIF – www.gbif.org), Fishbase (www.fishbase.org), and the International Union for the Conservation of Nature (IUCN – http://www.iucnredlist.org/technical-documents/spatial-data). Species in these databases were selected for inclusion in our analysis if there were at least 10 occurrences of them between 40°S and 40°N in the Pacific. Most species far exceeded this minimum threshold of records for inclusion (*i.e.,* median number of records per species = 1205). The common and scientific names of these species, as well as the number of species records, are listed in Supplementary Table 1. Records were removed from the dataset if there were null values, the spatial location was marked as “not assigned”, or when records were replicated among multiple databases. An environmental dataset based on the outputs of the three earth system models (IPSL-CM5A, GFDL ESM2G, and MPI-ESM-MR) was assembled for the RCP 2.6 and 8.5 scenarios. This environmental dataset was comprised of information on ocean temperature, salinity, oxygen, pH and NPP from the seafloor and the surface layer (0–100 m). Each environmental variable was interpolated spatially onto a 0.5° × 0.5° latitudinal/longitudinal

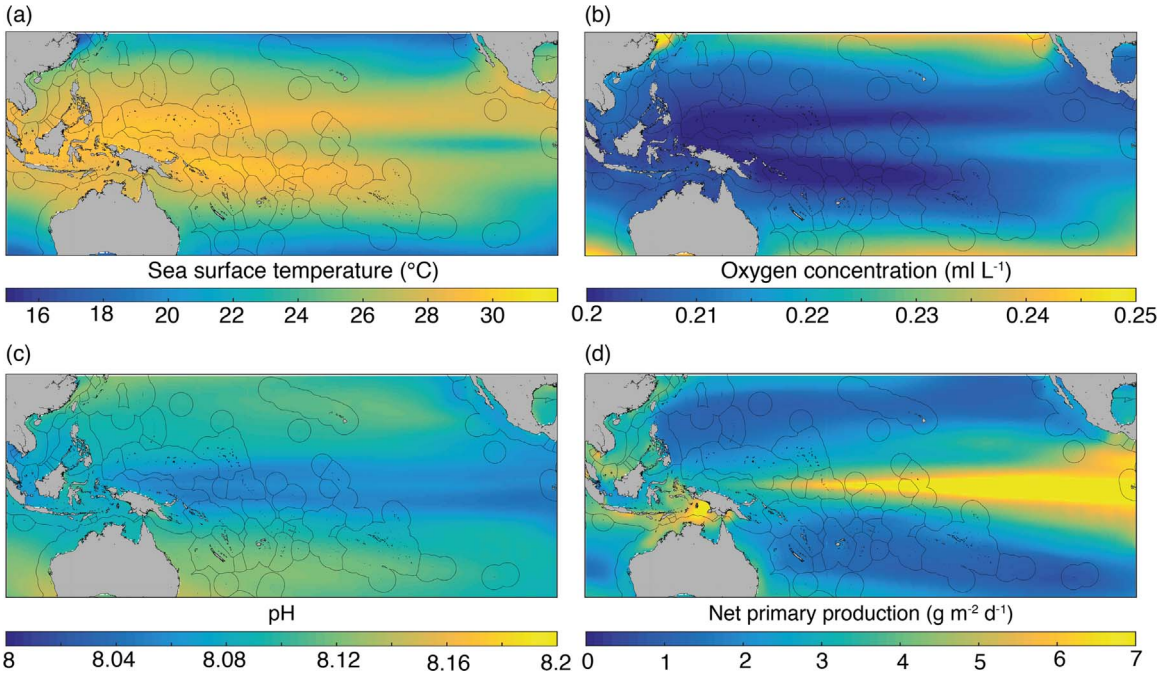

Fig. 1. Map of mean values of physical and biogeochemical variables for the period 1980–2000. (a) Sea surface temperature (SST), (b) surface oxygen concentration, (c) pH, (d) net primary production. Black lines indicate the Economic Exclusive Zones (EEZs) of Pacific Island countries and territories (PICTs).

grid for the years 1950–2100. A climatology of each of these variables was then computed for the 1980–2000 period.

A multi-model approach was adopted to best approximate the environmental niche of each species. Using presence only data, four environmental niche models (ENM) were applied to our dataset: the Bioclim and Boosted Regression Trees models from the Biomod2 R package [71], Maxent [57], and the Non-Parametric Probabilistic Ecological Niche (NPPEN) model [5]. Only models with an Area Under the Curve (AUC) value > 0.7 were considered in the ensemble for a given species, climate scenario, and earth system model. The spatial distribution of each species from the four ENMs was averaged annually over the years 1950–2100 and also over the three time periods of interest: 1980–2000, 2040–2060, and 2080–2100.

Species richness (*i.e.*, alpha diversity) was computed by numerically identifying a probability threshold of confirmed occurrence of a species based on the mean ENM habitat suitability index (HSI) from 1980 to 2000. The threshold for the occurrence of each species was set at the 25th percentile of the HSI distribution using data from the 1980–2000 period. If HSI was greater than or equal to the threshold, the species was considered present. Species richness was subsequently computed by summing the number of species present in each grid cell over each time period.

To assess potential changes in marine biodiversity driven by climate change, two indices were computed: local species gain and local species extinction [44]. Local species gain is the number of novel species that occurred in a geographical area where they were not previously found during a reference period (1980–2000). Local species extinction represents the number of species no longer found in a geographical cell where they previously occurred during the reference period. Maps of species gain and local extinction were produced for both RCP scenarios for the years 2040–2060 and 2080–2100. In addition to examining these two metrics for all species occurring in our study region, species gain and local extinction were also examined specifically among exploited pelagic species and reef-associated species.

2.3. Maximum catch potential (MCP)

Changes in maximum catch potential (MCP) of exploited marine fishes and invertebrates were projected using a dynamic bioclimate envelope model (DBEM). The model is a mechanistic species distribution model that simulates changes in growth, reproduction, body size, dispersal and abundance of species based on species biology, habitat preferences, environmental conditions, and fishing (see [24] for a detailed description of the model). Model parameters related to habitat associations, intrinsic population growth rates, and length-weight relationships were obtained from FishBase (www.fishbase.org) and SeaLifeBase (www.sealifebase.org). The main environmental variables considered by the model included seawater temperature, oxygen concentration, pH, NPP, surface ocean currents, and salinity. Projected values of these variables were examined for RCPs 2.6 and 8.5 from each of the three earth system models. Species distribution was projected onto a 0.5° latitude × 0.5° longitude grid of the world ocean. For each species and grid cell, simulations were made of changes in the species' MCP - a proxy for maximum sustainable yield. Since populations are modeled by a logistic growth model, the fishing mortality required to achieve MCP in each year was calculated using the intrinsic population growth rate and was then applied to the DBEM to simulate fisheries catches [24]. A total of 328 species of fishes and invertebrates that were reported in fisheries catch records (www.seaaroundus.org) in the Eastern and Western Central Pacific (Food and Agriculture Organization statistical areas 71 and 77) was analyzed here. A complete list of these species is included in supplementary material from Cheung et al. [21]. For the 2040–2060 and 2080–2100 periods, changes in total MCP, pelagic species MCP, and demersal (typically reef-associated) species MCP were calculated across the tropical Pacific relative to the baseline years 1980–2000.

3. Results

3.1. Physical and biogeochemical oceanic variables

Several of the physical and biogeochemical oceanic variables analyzed here shared similar biogeographic patterns during the baseline period (Fig. 1). Across the study region, mean annual SST during this period varied between 15–32 °C, displaying a spatial gradient where mean SST decreased moving poleward. SST was also cooler in the

Eastern Pacific equatorial upwelling zone. Maximum mean annual SST was observed in the western Pacific warm pool located in the region around Indonesia and Papua New Guinea. Due to the fact that temperature influences how much oxygen can be dissolved in seawater, these two variables displayed inverse spatial patterns, such that regions characterized by warm temperatures contained a lower surface concentration of dissolved oxygen. Surface pH varied between 8 and 8.2 across the study area, with the lowest mean annual pH occurring in the Eastern Tropical Pacific and the equatorial upwelling zone. Both of these regions are characterized by upwelling of nutrient-rich water in which organic matter has been re-mineralized releasing dissolved CO_2 and lowering the pH of seawater. The equatorial upwelling zone was also characterized by elevated NPP ($> 5\ g\ m^{-2}\ d^{-1}$). Increased primary production was also observed in areas with extensive continental shelves. Outside of these regions, primary production tended to range between ~1–3 $g\ m^{-2}\ d^{-1}$.

Under the RCP 8.5 scenario, most regions of the tropical Pacific were projected to warm by 1–2 °C by the year 2050 and ≥ 3 °C by 2100 (Fig. 2 and S1). Areas with the most rapid rate of warming included the equatorial upwelling zone, the inter-tropical convergence zone, parts of the Northwestern Hawaiian Islands, and southern Japan. The slowest rate of warming in this region was projected to occur in the area surrounding Easter Island.

Due in part to temperature's influence on the solubility of oxygen in seawater, the warming projected to occur throughout the 21st century was accompanied by declines in surface dissolved oxygen (Fig. 2 and S1). Under the RCP 8.5 scenario, surface oxygen decreased by ≤ 0.008 ml L^{-1} across most of the study area by the year 2050, with these trends increasing over time. The spatial patterns associated with projected changes in dissolved oxygen were similar to those observed for SST.

Accompanying this decline in oxygen concentration, pH was projected to decrease by about 0.15 units under the RCP 8.5 scenario by the year 2050 (Fig. S1), with decreases of 0.25–0.4 pH units projected for the year 2100 (Fig. 2). Compared to other physical and biogeochemical variables, these changes in pH showed relatively little spatial variability, although declines in pH were projected to be slightly lower in the area surrounding the equator.

Most PICTs were projected to experience declining NPP throughout the 21st century (Fig. 2 and S1). Under the RCP 8.5 scenario, the largest declines across our study area were projected to occur in the equatorial upwelling zone. A few isolated areas (*e.g.*, Easter Island, west of the Clipperton Islands, parts of Indonesian waters) were projected to experience increases in NPP by the year 2100 under RCP 8.5. Generally, spatial patterns were similar for this emissions scenario in the years 2050 and 2100, but the decline in primary production was exacerbated in later years.

The direction of changes in these four oceanic variables and their spatial patterns were largely similar under the RCP 2.6 and RCP 8.5 scenarios. However, due to the lower emissions of greenhouse gases under RCP 2.6, the changes experienced across all four variables were much smaller. For example, SST warmed by ~1 °C across most regions

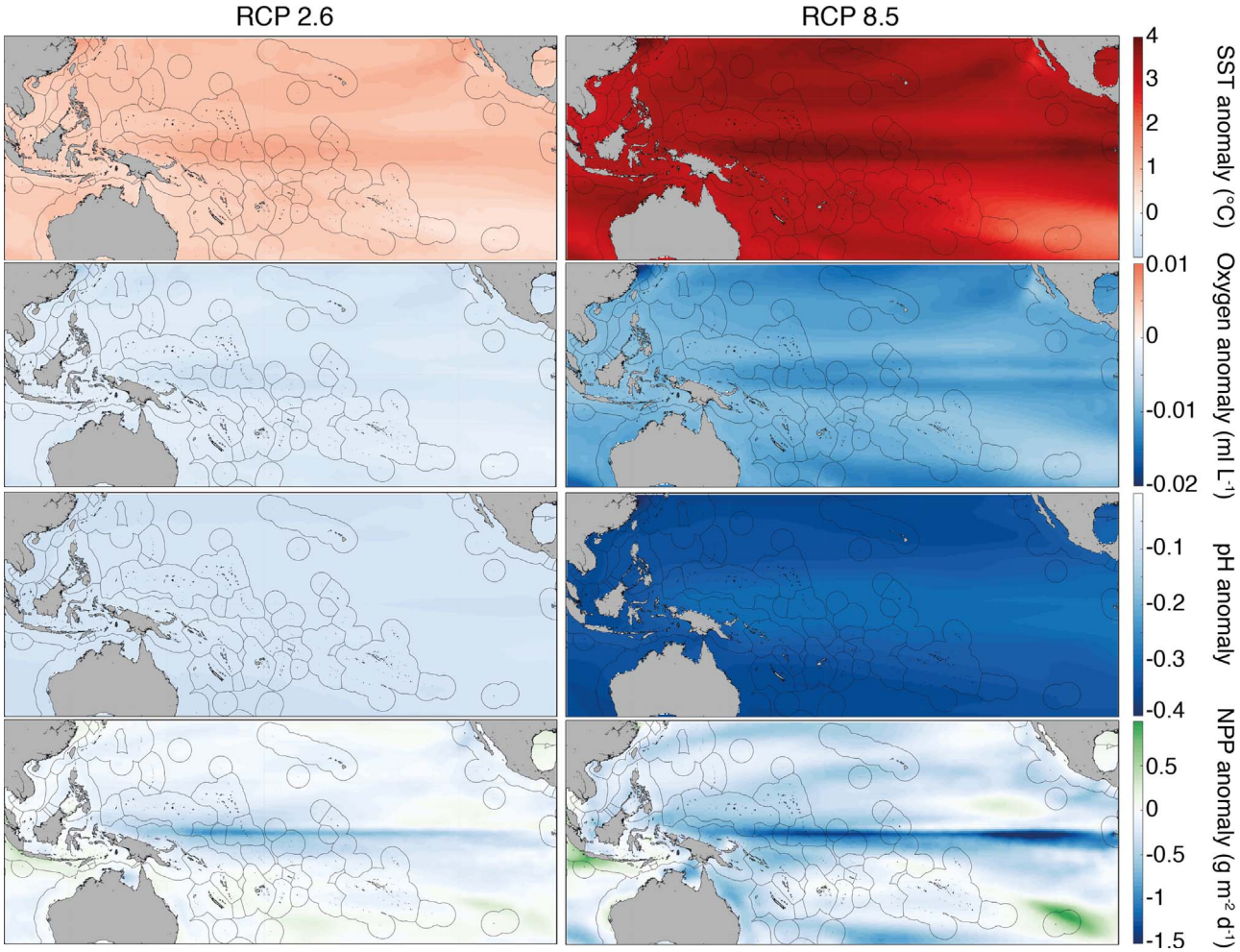

Fig. 2. Maps of changes in environmental conditions by the years 2080–2100. Physical and biogeochemical variables displayed here include sea surface temperature (SST), surface dissolved oxygen, pH, and net primary production (NPP) from Representative Concentration Pathways (RCPs) 2.6 and 8.5. Anomalies are relative to the baseline period shown in Fig. 1. Black lines indicate the Economic Exclusive Zones (EEZs) of Pacific Island countries and territories (PICTs).

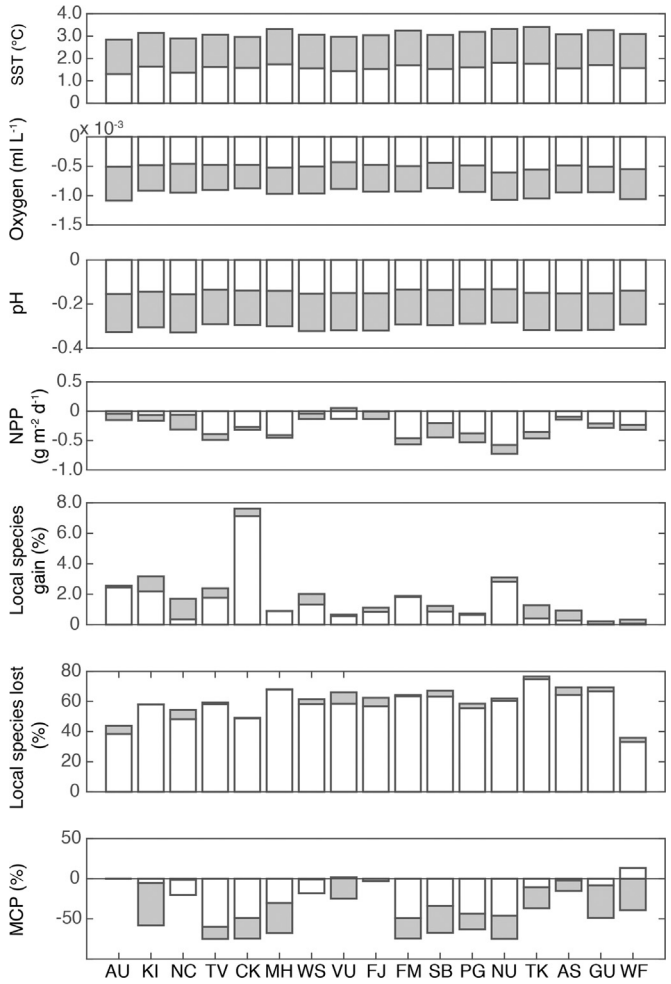

Fig. 3. Projected changes in ecosystem drivers, biodiversity and maximum catch potential at the country level. Changes are shown for the 2040–2060 (white bars) and 2080–2100 (grey bars) time periods, where the percent change is calculated relative to the 1980–2000 baseline under the RCP 8.5 scenario. Abbreviated country names: AU-Australia, CK - Cook Islands, FJ - Fiji, KI - Kiribati, MH - Marshall Islands, FM - Micronesia, NC - New Caledonia, NU - Niue, PG - Papua New Guinea, WS - Samoa, SB - Solomon Islands, TV - Tuvalu, VU - Vanuatu, TK - Tokelau, AS - American Samoa, GU - Guam, WF - Wallis and Futuna.

by the year 2100 under RCP 2.6, whereas the rate of warming approximately tripled under RCP 8.5 (Fig. 2). Similarly, by 2100 changes in other oceanic variables were reduced by 2–4 fold under the RCP 2.6 scenario in comparison with RCP 8.5.

At a country level, projected centennial changes in SST, dissolved oxygen, and pH were fairly uniform, displaying relatively little spatial variation (Fig. 3). Under RCP 8.5, all PICTs were projected to experience nearly a 3–4 °C increase in SST by 2100, whereas country-specific temperatures rise by 1–2 °C by 2050. Across all countries, oxygen concentration was projected to decline by 0.005–0.007 ml L^{-1} by 2050, with declines approaching or exceeding 0.01 ml L^{-1} by 2100. The largest changes in surface oxygen were projected to occur in Australia, Wallis and Futuna, Niue, and Tokelau. A spatially uniform decline of 0.17–0.19 pH units was observed across all countries by the year 2050, with declines rising to 0.3–0.4 pH units under RCP 8.5 by 2100. Compared to these other physical and biogeochemical variables, changes in NPP exhibited greater spatial variability at the country scale (Fig. 3). During the 2080–2100 period, Vanuatu was the only country projected to experience a slight increase in NPP. All other PICTs experienced declines in NPP throughout the 21st century under the RCP 8.5 scenario, with the largest decline projected to occur in Niue.

3.2. Ocean biodiversity

The tropical Pacific is a global hotspot of marine fish biodiversity. The general spatial pattern of biodiversity over the region reveals a strong concentration of species in coastal areas with a decreasing latitudinal diversity gradient in both coastal and the open-ocean ecosystems (Fig. 4a). The region is host to the "triangle of marine biodiversity" [12], which includes the coasts of Papua New Guinea, Indonesia, and the Philippines where the greatest concentration of coral reefs is located and, hence, the highest peak in reef-associated fish and invertebrate diversity. Local hotspots of diversity can be also found surrounding all tropical Pacific islands, the Great Barrier Reef, parts of the northern coast of Australia and the Arafura Sea. Open-ocean biodiversity represents on average 10% of the total species identified in the area. The highest number of open-ocean species is located in the Pacific tropical countercurrent, Coral Reef Triangle, and Eastern Tropical Pacific, while the lowest diversity is found in the subtropical gyres (Fig. S3).

The largest projected change in species richness was located in open-ocean areas with potential local species extinction reaching 80% by 2100 compared to the reference period (Fig. 4b, S2, and S3). The most impacted areas were located between 10° S and 32° N next to the subtropical frontal systems and at the edge of subtropical gyres. Local species gain in the open ocean reached a maximum of 20% by 2100 and was mostly located at the edge of the warm pool and the boundary of temperate marine systems. Coastal areas will be impacted by a 5–20% species loss on average by 2100 and a species gain ranging between 1 and 6%, with gains occurring mostly next to the northern Australian coast and Arafura Sea. These patterns of change were consistent for both diversity indices and emission scenarios suggesting that the species reported here were sensitive to small modifications in the environment. This pattern was related to the extirpation of marine species from endemic sites owing to a change in their optimal environmental conditions that the species attempted to track by migrating poleward.

When these projections were parsed out separately for pelagic and reef-associated species (Figs. S3-S4), spatial patterns of local species gain and extinction were quite similar for total species richness and pelagic species. Among reef-associated species, the greatest local species gains were projected to occur in the Arafura Sea, Gulf of Thailand, and west of Indonesia [Fig. S4(b)]. Local species extinctions reached their maximal level for reef-associated species in the East China Sea, Gulf of Thailand, and west of Indonesia [Fig. S4(c)].

At the country level, most PICTs experienced local species gains of less than 4%, with the exception of the Cook Islands where the local species gain approached 8% by the year 2100 under RCP 8.5 (Fig. 3). In contrast, local species losses were much larger across all countries typically exceeding 40%. These losses were particularly large in Tokelau, American Samoa, Guam, the Marshall Islands, Vanuatu, and the Solomon Islands, where local extinction rates approached 70% or greater.

3.3. Maximum catch potential (MCP)

Across the study area, the highest levels of MCP were associated with the continental shelf surrounding coastal areas and islands (Fig. 5a). The greatest peaks in MCP were observed off the coasts of China, Vietnam, the Philippines, Malaysia, Indonesia, Thailand, and, in the Eastern Pacific, the Gulf of California.

MCP was projected to decrease substantially in the tropical Pacific under climate change (Fig. 5b). More specifically, projections of MCP declined in most parts of the central Pacific by 2050 under both the RCP 2.6 and 8.5 scenarios. Relative to the 1980–2000 reference period, mean MCP across models was projected to decrease by more than 50% in the equatorial western Pacific under RCP 2.6 by 2050. By the year 2100, the total area with a substantial decrease in MCP (> 50%) expanded spatially by 36.0% under RCP 2.6 and by 74.4% under RCP 8.5.

Maps of changes in MCP were also produced separately for pelagic

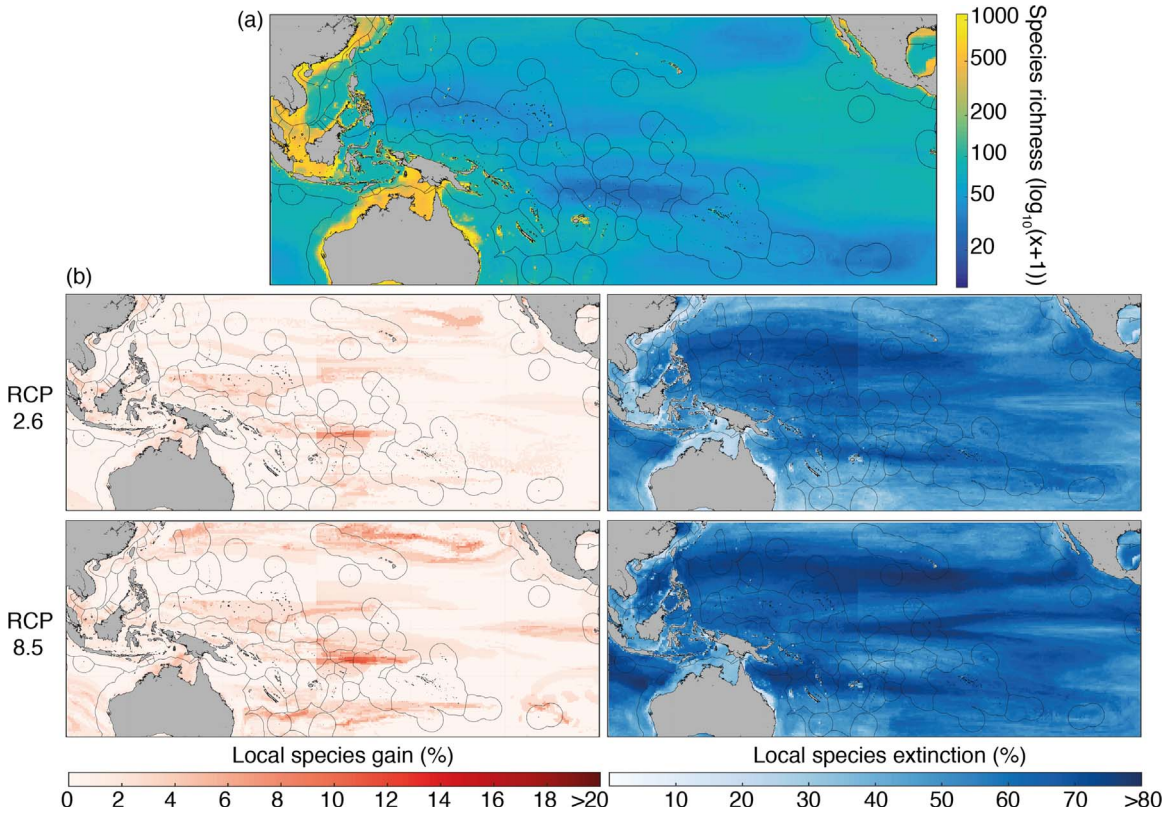

Fig. 4. Maps of changes in species richness under different climate change scenarios. (a) Mean species richness for exploited species for the 1980–2000 period; (b) local species gain and local species extinction. The maps in (b) are for mean values during the 2080–2100 period for Representative Concentration Pathways (RCPs) 2.6 and 8.5.

and demersal fish species (Figs. S5-S6). While both pelagic and demersal species MCP was greatest in coastal areas, spatial patterns differed such that maximum MCP occurred in the coral triangle for demersal fishes, whereas the maximum was observed at higher latitudes for pelagic species. Nevertheless, both categories of fishes responded similarly to climate change in that the greatest decreases in MCP were projected to occur in the western warm pool and central equatorial Pacific, with increases in MCP seen in parts of the eastern Pacific at higher latitudes. This pattern became increasingly amplified under the more extreme emissions scenario (*e.g.*, RCP 8.5) and during the later years of our projections. Generally, the magnitude of changes in MCP was slightly larger and more widespread for demersal species than they were for pelagic fishes.

The MCP in almost all PICTs was projected to decrease under both RCPs 2.6 and 8.5 and both time periods (Fig. 3). PICTs that showed the largest decrease in catch potential included Kiribati, Tuvalu, the Cook Islands, the Marshall Islands, Micronesia, Solomon Islands, Papua New Guinea, Niue, and Guam. In these countries and territories, MCPs in the Exclusive Economic Zones (EEZ) were projected to decrease by more than 50% by 2100 relative to 1980–2000 under RCP 8.5. By 2050, the projected decrease in MCP for Tuvalu, Cook Islands, Micronesia and Niue had already exceeded 50%, highlighting the high sensitivity of these countries to climate change impacts on their fisheries. In Wallis and Futuna, MCP was projected to increase slightly (around 10%) by 2050, later declining by the year 2100.

4. Discussion

Projected environmental changes in the tropical Pacific are considered to be some of the most severe in the global ocean according to the IPCC, especially when these changes are considered in the context of the low natural climate variability in this region [69]. Our results indicated that the region will be subject to warming of sea surface temperature, acidification of surface waters, a decrease in oxygen concentration, and declines in NPP. While the magnitude of these changes are not necessarily the largest at a global scale for each individual variable, the changes in temperature and pH will exceed their historical level of natural variation in the area by the mid 21st century [66]. Furthermore, the combined changes across biogeochemical variables can create a novel set of multivariate abiotic conditions that could define a new type of habitat that has not been experienced by tropical Pacific ecosystems during the period of observational records. Due to the joint effects of its high historical temperature and future increases in temperature (Figs. 1 and 2), this novel climate will be centered in the tropical band, mostly in the western Pacific warm pool. Similar to our results, a univariate analysis of climate velocity has also projected that novel climatic conditions could cause organisms to shift their range away from the tropical Pacific [18].

The projected changes in physical oceanographic and biogeochemical variables described herein updates the work of Ganachaud et al. and Le Borgne et al. [34,48] who analyzed changes in a similar suite of variables using the Special Report on Emission Scenarios (SRES) from the fourth IPCC report. Due to the adoption of the RCP scenarios with the fifth IPCC report, our results are not directly comparable to those of Ganachaud et al. and Le Borgne et al. [34,48], although all three studies examine the contrast between high (*i.e.*, RCP 8.5 and SRES A2) and low (*i.e.*, RCP 2.6 and SRES B1) emissions scenarios. With regard to SST, our high-end emissions projection for the year 2100 indicates greater warming across this region than the projections from Ganachaud et al. [34], reflecting in part the fact that more anthropogenic CO_2 is released under RCP 8.5 than SRES A2. A bias in the location of the western Pacific warm pool that is common among climate models used in the fifth IPCC assessment report may also be responsible in part for this projection of heightened warming [16]. However, our mid-century projections of SST changes are in line with those of Matear et al. [52] who used a bias correction scheme to compensate for model biases in

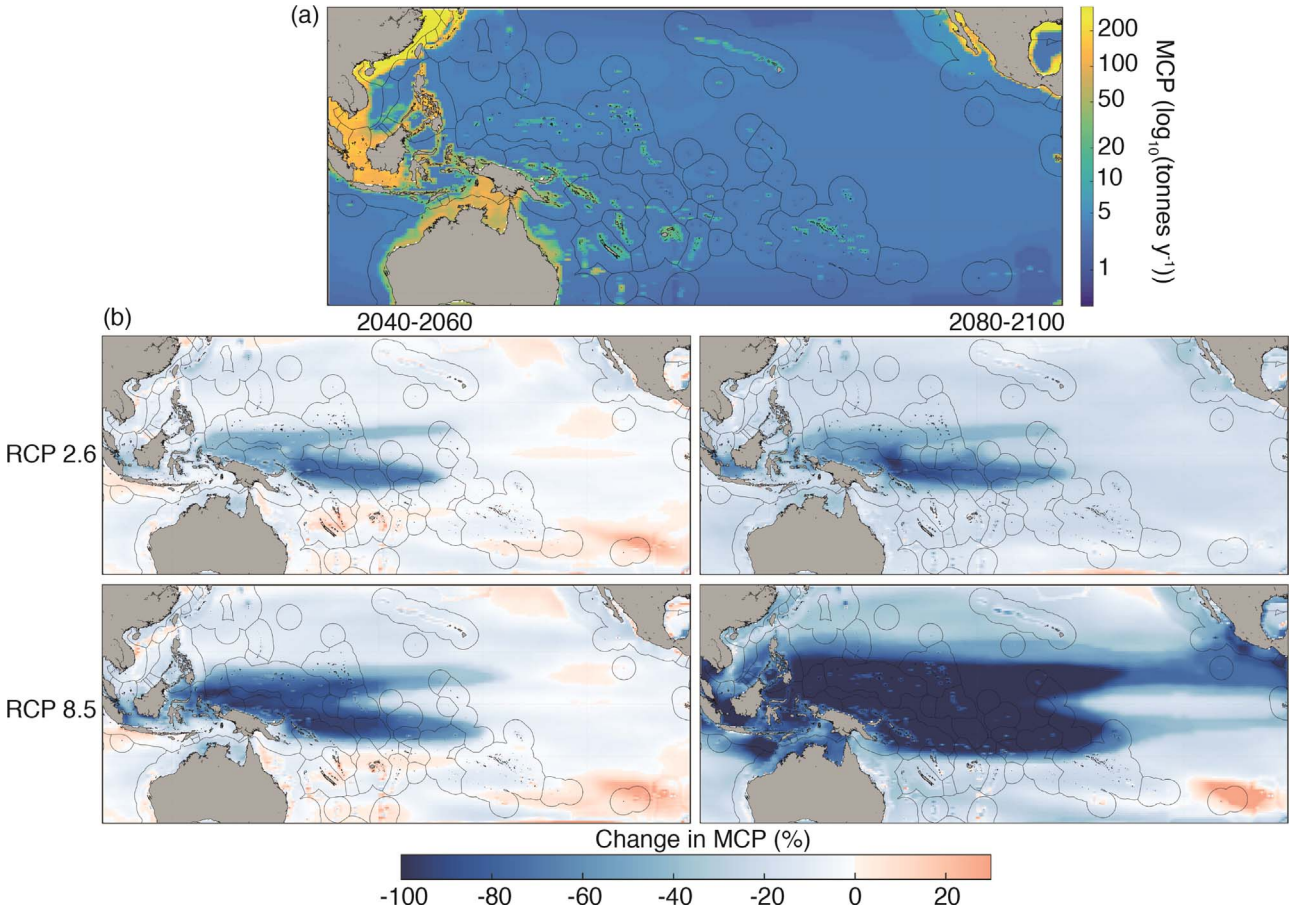

Fig. 5. Maps of projected Maximum Catch Potential (MCP) during different periods. (a) Mean MCP for the 1980–2000 reference period. (b) Change in MCP during 2040–2060 and 2080–2100 under Representative Concentration Pathways (RCPs) 2.6 and 8.5 in comparison to the reference period.

the western tropical Pacific. Comparability between our projections and those of Ganachaud et al. [34] are more limited for oxygen and pH anomalies because different depth horizons were examined and different indicators of changes in the oceanic carbon cycle were analyzed. Nevertheless, it does appear that there could be some discrepancies in biogeographic patterns since our research identified a fairly uniform decrease in surface oxygen concentration across the region while Ganachaud et al. [34] noted that dissolved oxygen may increase at depth in the Pacific Equatorial Divergence due to decreased remineralization of organic matter. When examining projected changes in NPP, the spatial pattern of our results also differs in some details from those of Le Borgne et al. and Matear et al. [48,52]. Le Borgne et al. [48] projected a slight increase in NPP in the Pacific Equatorial Divergence whereas our updated results and those of the high-resolution model of Matear et al. [52] both reported a substantial decline in NPP in that region. However, our results diverged from Matear et al. [52] in the western Pacific warm pool where their model projected increased NPP reflecting a greater supply of nutrients to the photic zone.

Marine species distribution and temporal dynamics are largely influenced by environmental conditions since marine species are ectotherms. Hence, the projected novel habitats are expected to influence ecosystem structure (*e.g.*, biodiversity) and services (*e.g.*, maximum catch potential). This analysis examining 1091 species reveals a large decrease in local biodiversity driven by species loss in the tropical band, as well as a decrease in potential catch in the same region. This change in species distribution and abundance emerges from the extent of species' environmental tolerance and the statistical and mechanistic relationships between species abundance and biogeochemical variables. Here the distribution of each species is computed following ecological niche theory as proposed by Hutchinson [41] and subsequently is a result of the tolerance range that is calculated using present-day spatial records of each species and its associated conditions. Therefore, if the multivariate conditions that occur in an area are not within the tolerance range of a species, the probability of species occurrence and its abundance are expected to be low. However, this numerical procedure assumes that no physiological adaptation is possible and that the full environmental tolerance range of each species is captured by the observed geographical records.

The species most affected by environmental change are endemic species with a narrow spatial distribution that occur in tropical regions. These species are adapted to low seasonal fluctuations typical of tropical climates and are often adapted to specific habitats, such as corals or seagrass beds. Thus, their tolerance range of environmental conditions will be narrow due to hyper-specialization. Also, their occurrence in areas with present-day maximal temperatures when examining climatological conditions at a global scale results in a high vulnerability to any further warming. These species principally consist of reef-associated fishes and are mostly localized in coastal areas. Among coastal fisheries targeting reef fishes, the largest declines in MCP (> 80% under the high gas emission scenario) were projected to occur in the western tropical Pacific.

In contrast to these results for coastal fisheries, highly migratory species, such as tunas and billfishes, can be found in tropical, temperate, and polar ecosystems and are typically characterized by a wide spatial distribution with a tolerance of a large range of environmental conditions [63]. The more widely distributed a species is the more likely that the effect of climate change will have a minimal influence on its distribution. For instance, the distribution of yellowfin tuna (*Thunnus albacares*) is more likely to be affected by a change in environmental conditions since this species is mostly adapted to tropical

regions in comparison to albacore (*Thunnus alalunga*) and bluefin tuna (*Thunnus thynnus*), which are more widely distributed [14,17,47,67]. Some support for this hypothesis is provided by Robinson et al. [65] who modeled changes in habitat suitability for these species under climate change. With regard to yellowfin tuna and skipjack tuna (*Katsuwonus pelamis*), the two species with the most lucrative fisheries in this region, DBEM projections indicate that both fishes will shift their distribution eastward and poleward throughout the 21st century, with the potential disappearance of these species altogether from the western warm pool region where novel climatic conditions emerge. These results are qualitatively consistent with projections for these species made using the Spatial Ecosystem And Populations Dynamics Model (SEAPODYM), which was designed specifically to examine changes in tuna fisheries in response to climate change and climate variability [10,49].

Decreases in species richness and catch potential can affect income, livelihood, food security, and political stability of tropical PICTs [7]. Pelagic fishery operations, including catches, fish processors, and licensing fees for foreign fleets, contribute considerably to the gross domestic product (GDP) and government revenues of many PICTs [7]. A decrease in catch potential would reduce revenues generated from these fisheries and associated businesses [46]. Small-scale coastal fisheries also contribute substantially to subsistence and livelihoods in this region; such contributions may have been largely underestimated in official statistics [75]. The projected local extinction of several reef-associated species may substantially reduce seafood availability to coastal communities in the regions that are generally highly nutritionally vulnerable [38]. Moreover, eco-tourism is an important industry in some of the PICTs, such as Palau [76]. Decreases in fish diversity and the degradation of coral reefs from projected warming and ocean acidification are likely to reduce the attractiveness of the tropical Pacific to international tourists. In addition, the pelagic fish stocks in the tropical Pacific straddle the EEZs of multiple nations and territories. The projected shift in distribution and abundance of tunas and billfishes could destabilize transboundary fisheries agreements and management in the region, resulting in international disputes and conflict in fisheries resource sharing [53].

The projections presented in the paper may be affected by uncertainties in the parameters and structure of earth system and biological models; however, the high vulnerabilities of the marine biodiversity and fisheries in the tropical Pacific region highlighted by this study should be robust to these uncertainties. Firstly, although the projected changes in ocean conditions vary between earth system models, the tropical Pacific was consistently highlighted as having large changes in the combined set of ocean variables relative to other areas in the Pacific Ocean. All the earth system models considered here do not have sufficient resolution to fully resolve coastal processes, affecting the representativeness of the projections for coastal and shelf seas [68]. On the other hand, most countries and territories in the tropical Pacific have a narrow insular shelf and the condition of their waters is more representative of the surrounding open oceans that are better represented by the earth system models. Secondly, the structure of the species distribution model that generated the projected changes in biodiversity and fisheries catch potential contributed to uncertainties of the projections [25]. However, inter-comparison of different species distribution model projections with different earth system models show that all the models used in this study are in agreement in identifying the tropical Pacific as having high risk of impacts to biodiversity and fisheries under climate change [24,44]. Important model structural uncertainties remain in the projections particularly with regards to the effects of trophic interactions, multiple stressors resulting from other human activities, and the ability of marine species to adapt to and tolerate the novel environmental conditions in the tropics [25]. Analysis of historical fisheries data suggests that ocean warming may have already driven changes in catch composition that are in agreement with the projections presented in this study [22]. Thus, the high vulnerability of marine biodiversity and fisheries in the tropical Pacific as revealed by model projections should be robust while the magnitude of the projected changes is more uncertain.

While mitigation of greenhouse gas emissions at the global scale is clearly needed, several regional actions can be taken to minimize the disruptive impacts of climate change on fisheries, economic livelihoods, and food security. First, conflicts between fishing nations due to changes in distribution of highly migratory fish species can potentially be avoided through trading country-based allocations of fishing effort in the regional 'vessel day scheme' [8]. Such a scheme is already in place for tuna species and has helped PICTs cope with interannual variability in fish distribution associated with El Niño Southern Oscillation (ENSO) [7].

Second, networks of marine protected areas (MPAs) arranged as "stepping zones" may help ensure connectivity between fish populations by facilitating migration of fishes to new areas with adequate conditions for their survival in a changing ocean [51,64]. MPAs that conserve important habitats used by fishes, such as estuaries, coral reefs, mangroves, and seagrass beds, can ensure that fishes have a place to migrate to as oceanic conditions change. For demersal and reef-associated species, dispersal between protected areas is more likely to occur during a fish's larval stage, thus motivating the need to protect the habitat of recently settled juvenile fishes in the network of MPAs. Juvenile fish habitat can also be protected by reducing the influx of sediment, pollutants, and excess nutrient loads from land into coastal catchments [10]. While such fish population connectivity achieved through networked MPAs and other habitat conservation measures may not deter local species extinction, it could ensure continued viability of species across their distributional range. However, the benefits of networked MPAs in terms of facilitating poleward latitudinal shifts may also be limited by the fact that there are few places for new coral reefs to be established due to lack of hard substrata in the euphotic zone and because ocean acidification impacts of climate change are expected to be more severe at higher latitudes [73]. Also, in some cases, biogeographic boundaries may prevent dispersal to suitable habitats from taking place.

Third, coastal fishers, who often lack the capacity to travel far from shore tracking the changing distribution of fishes, may need to switch which species they target. Seasonal forecasting of fisheries [72] has the potential to benefit both coastal and offshore pelagic fisheries by providing timely alerts to fishers about the changing distribution of species in association with both climate change and climate variability. To ensure that overexploitation does not occur, seasonal forecasting of fish distribution, abundance, and/or phenology should be implemented only in fisheries that already have well-enforced harvest controls in place [31]. Within the tropical Pacific context, seasonal forecasts have the potential to aid disaster preparedness, help determine when tuna and other highly migratory fishes will be most accessible to fishers, and optimize aquaculture activities that have a seasonally varying component [11,30]. Further detailed recommendations regarding adaptations and supporting policies for responding to climate change impacts on tropical Pacific fisheries and aquaculture are described in Bell et al. [8].

5. Conclusions

Changing environmental conditions are anticipated to alter the marine environment surrounding PICTs in a multitude of ways. Increases in SST and declines in surface oxygen, pH, and NPP are projected throughout this region with these impacts accelerating throughout the 21st century, especially under the RCP 8.5 scenario. Under RCP 2.6, these physical and biogeochemical changes are projected to be similar, albeit less severe. Together these changes in temperature, pH, oxygen, and NPP alter the ecological niches available to commercially important fishes and invertebrates. This results in high levels of local species extinction under both climate change scenarios as species either move towards more suitable habitats or as abundance

potentially drops among species that are not capable of migrating. The species that become locally extinct are not replaced by as many new species moving into the area because relatively few species are adapted to the novel environmental conditions projected to occur in the western tropical Pacific by the end of the 21st century. When taken together, these factors result in a decline in MCP that exceeds 50% across much of the tropical Pacific under the RCP 8.5 scenario. Climate mitigation measures can serve to drastically improve this projected outcome, with fewer areas experiencing large decreases in MCP under RCP 2.6.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at http://dx.doi.org/10.1016/j.marpol.2017.08.015.

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